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ART. 13. SKULL VARIATION IN THE MEADOW VOLE
(*MICROTUS P. PENNSYLVANICUS*) IN PENNSYLVANIA

BY DANA P. SNYDER

INTRODUCTION

The delimitation of mammalian subspecies is quite generally based on proportional or absolute size differences as well as on qualitative characteristics which can not be readily measured with objectivity. There has, however, been some question whether such quantitative differences always supply valid evidence of genetic variation between two populations (Huxley, 1932; Reeve, 1940; Tryon, 1951). It is, of course, widely recognized that absolute size can be affected by environmental as well as by genetic factors, but it is perhaps less clearly realized that the ratio between two dimensions may be likewise unreliable. Such ratios may vary as the absolute size varies, and since we can not always evaluate size variation in terms of causal factors neither can we interpret the differences in proportions. Valid comparisons of proportions should take into account any differences in absolute size.

Opportunity for a study of this problem in relation to geographic variation has been provided by recent collections of mammals in Pennsylvania. The meadow vole, *Microtus p. pennsylvanicus*, is particularly well represented in the collections and has furnished the material on which this report is based. Only quantitative characters, chiefly skull dimensions, have been used; although in some preliminary treatment external measurements and weights were also analyzed. This report is concerned primarily with the amount and nature of the variation rather than with its cause.

The material studied is a part of the mammal collection of Carnegie Museum. Most of the specimens were collected by the Survey of Pennsylvania Mammals, a series of six Pittman-Robertson Projects (no. 20-R, 24-R, 37-R, 38-R, 42-R, and 43-R) conducted under the Federal Aid to Wildlife Restoration Act of 1937. The survey was a co-operative effort among the Pennsylvania Game Commission, the U. S. Fish and Wildlife Service, and Carnegie Museum. A final report has been published on each of the Pittman-Robertson Projects (Richmond and Rosland [sic] 1949; Grimm and Roberts, 1950; Roslund, 1951; Gifford and Whitebread, 1951; Grimm and Whitebread, 1952; Roberts and Early, 1952).

I wish to thank Dr. J. Kenneth Doult, Curator of Mammals, Carnegie Museum, for many helpful suggestions and criticisms during the study. For much valuable aid I am indebted also to Miss Caroline A. Heppenstall, Assistant Curator of Mammals, and John E. Guilday, Assistant Curator of Comparative Anatomy. Discussions with members of the biostatistics staff of the University of Pittsburgh School of Public Health have been most valuable to me. I should particularly like to thank Dr. D. G. Horvitz, Dr. D. J. Thompson and Dr. C. C. Li for their kind assistance. Responsibility for any errors or for any question of interpretation of results is, of course, mine. The illustrations were very ably drawn by Clifford J. Morrow, Jr. and by Charles L. Ripper. Cambridge University Press very obligingly allowed me



to quote from D'Arcy Thompson's "On Growth and Form." The quotation from "Growth in the Snout of Anteaters" is by permission of the Zoological Society of London.

NON-GEOGRAPHIC VARIATION

MEASUREMENTS

Weight and external measurements are those taken by the collector. Skull dimensions were recorded to the nearest 0.1 millimeter by means of dial calipers. Measurements were taken as described below and illustrated in Fig. 1. Paired structures were measured on the left side.

1. Greatest length of skull: maximum distance between the occipital condyle and the most anterior point of incisor.

2. Condylzygomatic length: distance between occipital condyle and antero-superior edge of zygomatic process of maxilla.

3. Length of nasal: maximum length of nasal bone.

4. Length of incisive foramen: maximum length of palatine slit.

5. Length of diastema: distance from posterior edge of incisive alveolus to anterior edge of alveolar space of molar row.

6. Length of rostrum: dimension obtained by subtracting condylzygomatic length from greatest length of skull.

7. Cranial breadth: distance between outer surfaces of the small squamosal bars (which form the ventral borders of the prelamdboidal fenestrations) taken at the point where, viewed perpendicularly from above, these bars pass beneath the overlying portion of the squamosal bone.

8. Interorbital breadth: least diameter of frontal bones between the orbits.

9. Zygomatic breadth: maximum spread of zygomatic arches.

10. Cranial height: perpendicular distance from highest point of parietals to a plane passing from most inferior point of auditory bullae along crown of most prominent molar (cf. Howell, 1924). To obtain this measurement the skull was placed on a glass plate as in Fig. 1, and the distance recorded from bottom of plate to dorsal-most portion of skull. The thickness of the plate was then subtracted to give the height.

SOURCES OF VARIATION

Considerable variability is found within samples from single localities. Two of the factors (age and sex) contributing to this non-geographic variation can of course be readily recognized and taken into account when populations from different localities are compared. Although variation due to sex can be completely eliminated (assuming correct sexing by the preparator), that resulting from age differences can usually be reduced only to some minimum value by grouping the specimens into narrow age ranges. The remaining variability, usually termed individual variation, perhaps reflects some local environmental differences (including seasonal differences in the environment) as well as the genotypic differences to be expected in a wild interbreeding population. The average value of this individual variation *within* each of two (or more) populations serves as a yardstick in determining the significance of the geographic variation *between* the populations.

Age variation. Howell (1924) in a study of individual and age variation in a local population of *Microtus montanus* found condylobasilar length to be the most satisfactory criterion on which to base a consecutive arrangement of the skulls in order of increasing development. Such a series can be arbitrarily divided into size groups which probably, in general, correspond to age groups. Such an arrangement based on a size measurement, although suitable for determining individual variation, is less desirable in a study of geographic variation. The character used (e. g. skull length) would be held constant, or at least be non-randomly selected, in samples being compared,

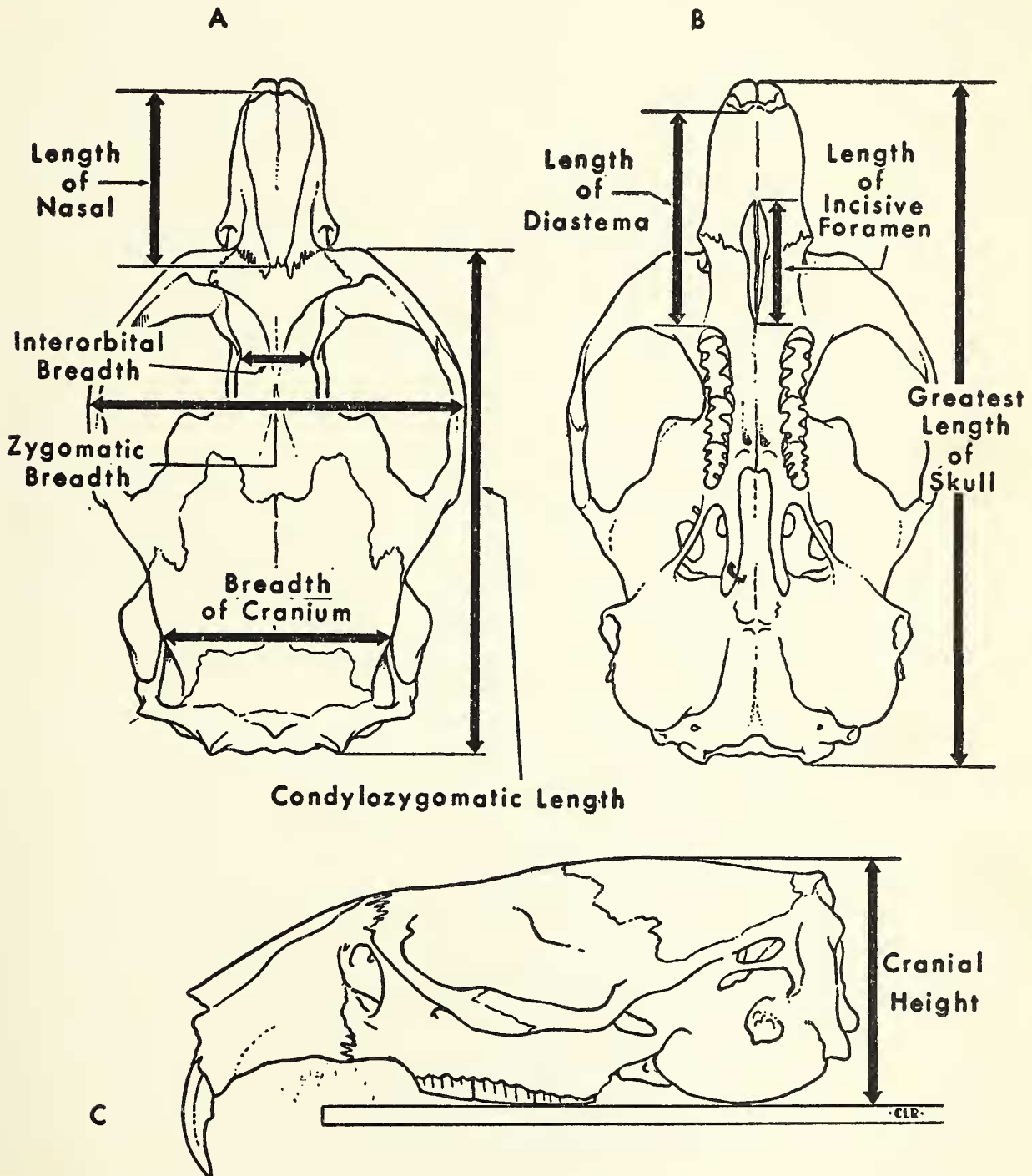


FIG. 1. Dorsal (A), ventral (B), and lateral (C) views of skull of *Microtus p. pennsylvanicus* illustrating dimensions explained in text.

and therefore no valid indication of geographic variation in this measurement could be obtained. Furthermore, conclusions regarding variation in other characters correlated with skull length would be open to question. As will be brought out later, it is desirable to compare samples in which one dimension, such as total length of skull, remains constant throughout. But it is well first to determine the actual geographic size variation among the populations and then to use more precise mathematical methods in reducing one dimension to a constant value for further investigations of variation in relative dimensions.

A more satisfactory aging method for some groups of mammals is the order and degree of suture closure and the development of crests and local prominences (See Doult, 1942 and references therein). Sutures, however, have not been of much aid in meadow voles because some suture lines disappear quite early while others remain apparent even in the oldest individuals available. To obtain satisfactory age groupings, it has, therefore, been necessary to rely on changes in characters which are more subjective in interpretation. Three characters, lambdoidal crest, mastoid-exoccipital crest, and paroccipital process, were finally selected for this purpose. In young animals the paroccipital process closely follows the curve of the auditory bulla but later becomes directed posteroventrally. In each skull examined the position of this process was assigned an arbitrary value of two, three, or four in order of increasing development. Similarly, each crest was given a value from one, representing least development, to four, showing maximum development. The three index figures thus assigned to each skull were then totaled to determine the age group to which the specimen belonged. There resulted nine such groups, the youngest represented by four (the smallest possible total value) and the oldest by 12 (the largest possible total value). These numbers representing the total values will hereafter be used to refer to the respective age groups. Although this method is subjective, the results should be comparable for all specimens studied by one worker.

It is possible that individual variation in these skull characters used to determine the relative age may be such that a wide age range is included in each age group with a consequent broad overlapping of actual ages from one group to the next. This condition, if subsequently found to be true, would not necessarily invalidate the method because the sample groups would still be statistically and biologically comparable under the assumption that for any given age group all samples would be normally distributed with the same actual mean age. In this event the variability due to age within each group would, however, be higher than desirable.

The mean and the range of greatest length of skull for the age groups 7 through 12 for a series from northwestern Pennsylvania are shown in Fig. 2. The age groups 4, 5, and 6 obviously represented quite young animals and were not used here or in further analysis. The successive increase in the mean from the youngest to the oldest groups, although it does not eliminate the possibility of overlap pointed out above, does indicate that the method gives an approximate age arrangement of the specimens. On the basis of the considerable individual variation indicated by the range of each

sample, it seems doubtful that a grouping on the basis of skull length would give a better approximation to the true age than the method employed here.

A further analysis was made of skull and external characters to determine which are least variable with respect to age. This analysis was based on a series from one locality (Pymatuning Swamp, Crawford County) in which

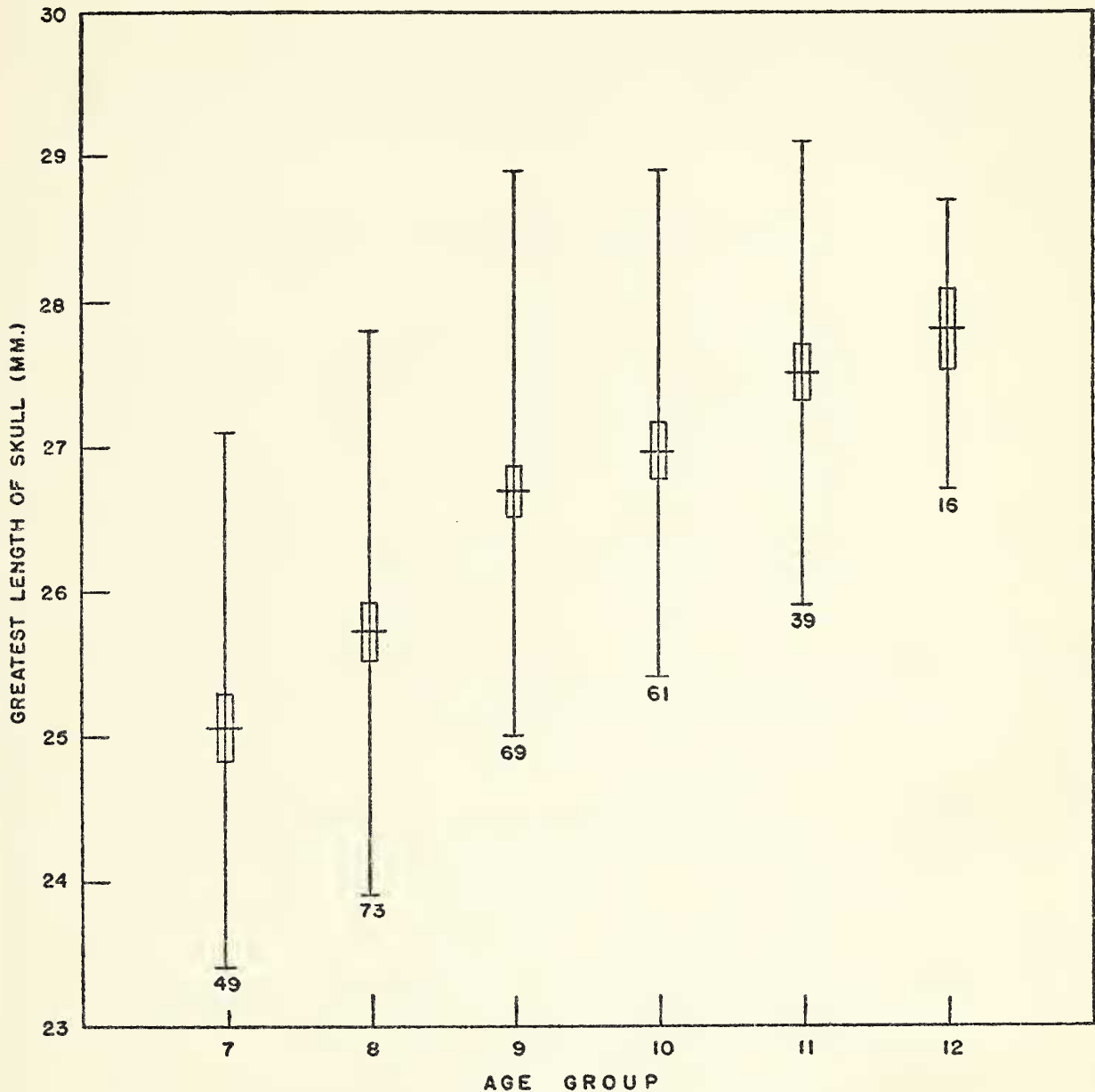


FIG. 2. Skull length of *Microtus p. pennsylvanicus*, age groups 7 to 12, males and females combined, from northwestern Pennsylvania. Range shown by light vertical line; number of individuals in sample by figures below this line; closed rectangle indicates two standard errors on each side of mean which is represented by the heavy horizontal line.

all age groups from seven to twelve were fairly well represented. Fig. 3 shows, for each character measured, the percentage of adult size (assumed to be represented by age groups 11 and 12) which specimens have reached at the earlier ages. Mean values are used in each case. Each plotted point is based on 12 or more specimens except for cranial height where because of damaged bullae, the number available was less ranging from 5 to 12 at

the various age levels. This graphical method is one developed by Simpson (1941) and the reader is referred to his paper for further explanation. It can be readily seen that cranial height, cranial breadth, and interorbital breadth approach their maximum development at an earlier age than do the other skull characters studied. Of the external measurements, ear and length of hind foot approach adult size earliest, and all four are essentially of adult size by age group 10. For external measurements, age group 10 should therefore be averaged with groups 11 and 12 in determining the base-line for adult size. However, this is unnecessary for the present purpose since the relative position of the other age groups would be only slightly affected.

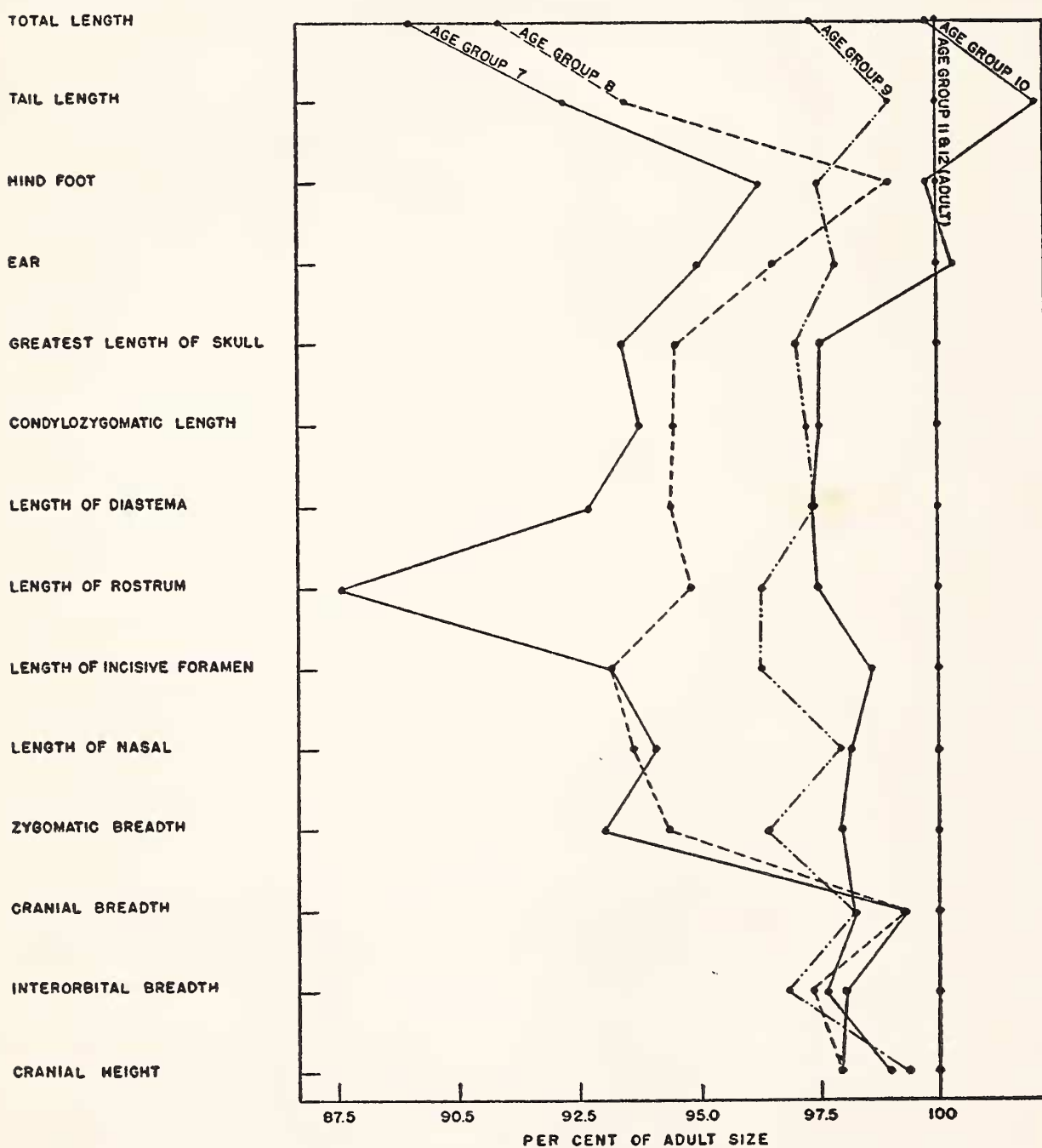


FIG. 3. Percentage of adult size (age groups 11 and 12) reached by *Microtus p. pennsylvanicus* (sexes combined) at earlier ages. Mean values of the dimensions at each age level were used in plotting.

TABLE 1

External and skull measurements, in millimeters, of *Microtus p. pennsylvanicus*, age groups 9-12, from Pymatuning Swamp, Crawford County, Pennsylvania. s_d is the standard error of the difference.

	MALES				FEMALES				MEAN δ - MEAN ♀ s_d
	Number in sample	Mean	Standard deviation	Coefficient of variation	Number in sample	Mean	Standard deviation	Coefficient of variation	
Total length	38	167.4 ± 1.2	7.4	4.42	26	164.4 ± 1.7	8.5	5.17	+ 1.50
Tail length	38	44.4 ± 0.9	5.7	12.84	26	44.1 ± 0.8	4.2	9.52	+ .23
Hind foot	60	20.6 ± 0.1	0.8	3.88	49	19.9 ± 0.1	1.0	5.03	+ 4.06**
Ear	38	14.0 ± 0.2	1.0	7.14	26	13.8 ± 0.2	1.0	7.25	+ 0.78
Weight	22	44.19 ± 1.34	6.29	14.23	11	43.96 ± 3.09	10.25	23.32	+ 0.08
Greatest length of skull	34	27.35 ± 0.11	0.63	2.30	24	26.80 ± 0.13	0.63	2.35	+ 3.28**
Condylozygomatic length	34	21.31 ± 0.09	0.52	2.44	25	21.00 ± 0.11	0.55	2.62	+ 2.20*
Length of nasal	30	7.70 ± 0.08	0.42	5.45	22	7.60 ± 0.06	0.26	3.42	+ 0.99
Length of incisive foramen ..	37	5.21 ± 0.05	0.28	5.37	26	4.99 ± 0.05	0.27	5.41	+ 3.12**
Length of diastema	37	8.34 ± 0.04	0.27	3.24	26	8.08 ± 0.06	0.30	3.71	+ 3.55**
Length of rostrum	34	6.04 ± 0.04	0.23	3.81	24	5.81 ± 0.05	0.23	3.96	+ 3.74**
Cranial breadth	52	11.03 ± 0.04	0.29	2.63	46	10.95 ± 0.04	0.28	2.56	+ 1.37
Interorbital breadth	58	3.66 ± 0.02	0.12	3.28	49	3.63 ± 0.02	0.16	4.41	+ 1.10
Zygomatic breadth	33	15.23 ± 0.08	0.47	3.09	27	14.98 ± 0.09	0.48	3.20	+ 2.03*
Cranial height	23	10.07 ± 0.06	0.27	2.68	20	10.06 ± 0.07	0.29	2.88	+ 0.12

*Probability between 5% and 1% levels

**Probability beyond 1% level

Secondary sexual variation. Sexual differences in absolute size in the Pymatuning Swamp specimens, shown in Table 1, are significant (probability between 5% and 1% levels) or highly significant (probability beyond 1% level) for several characters—length of hind foot, greatest length of skull, condylozygomatic length, length of incisive foramen, length of diastema, rostral length, and zygomatic breadth. For the measurement of length of skull, an analysis of variance between sexes was made using a total of 150 specimens from a number of localities in northwestern Pennsylvania. A mean difference of approximately 0.4 mm. was found to be highly significant throughout the area. On the basis of this information it seemed best to treat the sexes separately, and in further analysis of the data only males are used.

Individual variation. Individual variation in size, as indicated by the coefficient of variation was also determined for the series from Pymatuning Swamp. The results, given in Table 1, indicate the same relative variability as found by Goin (1943) for specimens from this area. The absolute values of the figures shown, however, are considerably lower than hers probably because of the more restricted age range of my samples.

The least variable skull measurements are the following—greatest length of skull, condylozygomatic length, cranial breadth, cranial height, and zygomatic breadth.

GEOGRAPHIC VARIATION

LOCAL VARIATION IN ABSOLUTE MEASUREMENTS

As a preliminary step in the analysis of state-wide variation, a study was made of local variation within a relatively small geographic area in northwestern Pennsylvania. In order to reduce age variation to a minimum and still obtain samples of sufficient size, it seemed desirable on the basis of the results shown by the graph (Fig. 3) to include only age groups 9 through 12 in each sample for all measurements except cranial height, cranial breadth, interorbital breadth, and length of hind foot. For a comparison of the latter characters age groups 7 through 12 were included. The variation contributed by this age spread was assumed to be sufficiently small so that any geographic variation present would not be obscured even though the age composition of each sample might be slightly different. Satisfactory samples were thus obtained from seven areas in northwestern Pennsylvania. These are indicated on the map (Fig. 4) by a solid circle where all specimens were taken at one locality and by an open circle in those cases where specimens were taken at a number of adjacent localities. Physiographically, two of the areas, A₁ and A₂, are situated on the lake plain of the Central Lowland Province; the other five are on the Appalachian Plateau. All are in regions which have been changed ecologically by agricultural activity. The meadow vole is distributed generally throughout this part of Pennsylvania being taken in fields, both cultivated and abandoned, and in grassy or marshy places which occur in low spots and along streams. Some of the habitat in the Crawford County area has been changed by the creation of Pymatuning Reservoir since the specimens were collected there.

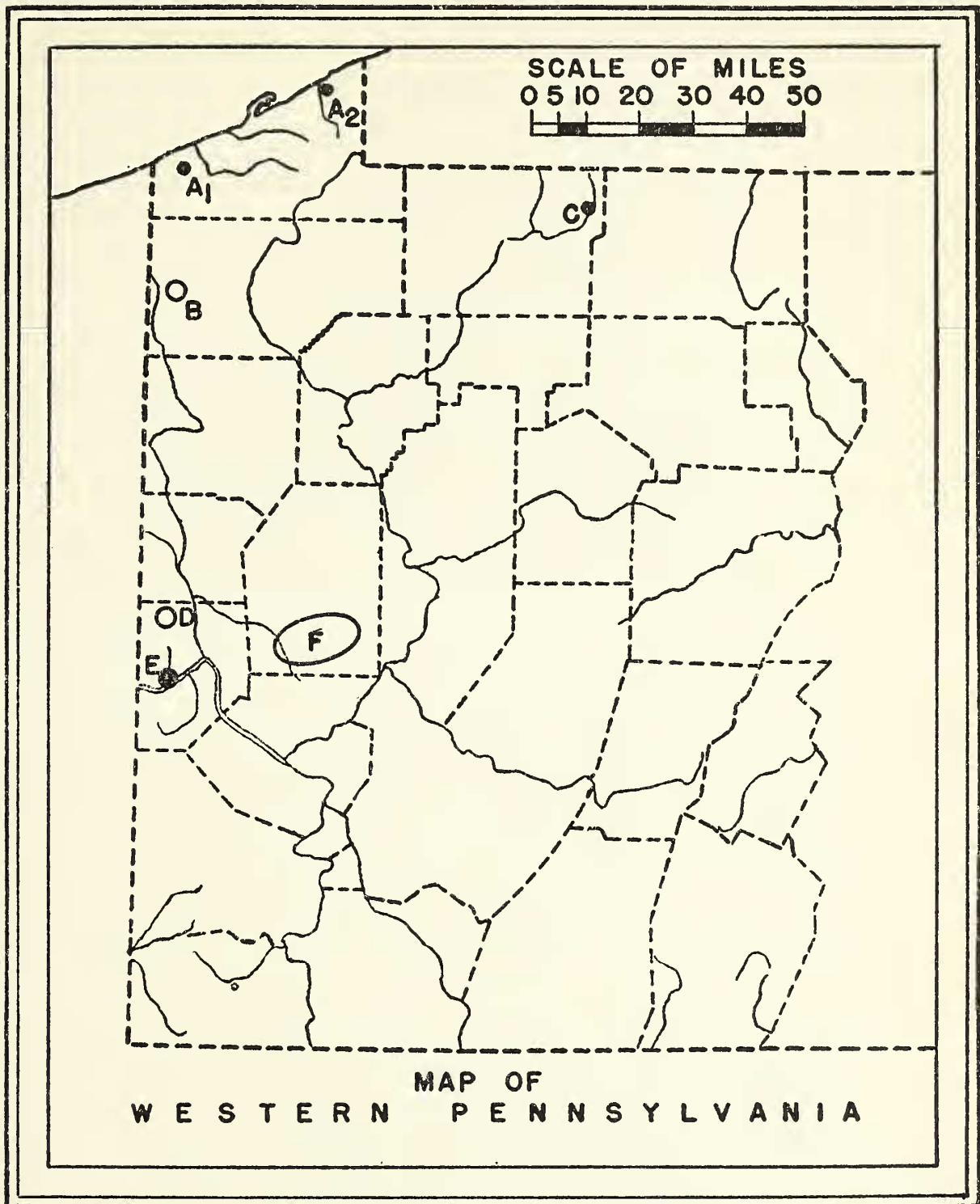


FIG. 4. Collecting areas represented by the seven samples used in analysis of local variation in *Microtus p. pennsylvanicus* in northwestern Pennsylvania. A₁, Erie Co., East Springfield; A₂, Erie Co., 4½ mi. SW. of Northeast; B, Crawford Co., Linesville, 4 mi. SE. of Linesville, 2 mi. SW. of Linesville; C, Warren Co., 2½ mi. N. of Kinzua; D, Beaver Co., ½ mi. NW. of New Galilee, 1 mi. NE. of Darlington; E, Beaver Co., 2 mi. E. of Industry; F, Butler Co., 2 mi. E. of Mars, 3 mi. E. of Mars, 2 mi. W. of Saxonburg.

The variation in skull length among these seven areas is shown in Fig. 5. It is obvious that considerable geographic variation occurs between areas which are quite near each other. Areas D, E, and F are all within a radius of 15 miles. It is also apparent that not all populations show such variation, even though they may be separated by greater distances. The variation in skull length as well as in a number of other dimensions was tested by an analysis of variance. The resulting ratios given in Table 2 show that, with the exception of cranial breadth and cranial height, variation within the area is highly significant. There is, accordingly, little reason to doubt the reality of appreciable phenotypic variation among populations within this relatively small area. Similar local variation has been notably demonstrated in *Peromyscus* (Sumner, 1932; Dice, 1940) as well as in many other diverse species of animals. Whether these differences are genetic, resulting from random gene fluctuations or from evolutionary pressures operating in slightly different environments, or whether they are non-genetic direct phenotypic expressions of environmental differences can not be readily determined. The studies of Sumner and of Dice cited above indicate that such differences may be hereditary. Tryon (1951) after an analysis of populations of pocket gophers in Montana believed that differences in length of skull might correctly be attributed to the effect of environment acting within genetic limits, but he also found evidence that some differences between local adjacent populations might be the result of reproductive isolation. It would seem most likely that both genetic and environmental differences are acting together to produce these populations showing morphological variation. Thus, an important problem is the partitioning of the observed variance into that portion caused by genotypic and that by environmental differences. If we are to base taxonomic conclusions on genetic as well as on morphological similarities or differences, it will eventually be necessary to discover the respective effects of environment and heredity in each situation studied. Such partitioning of the variance observed in wild populations is likely to be a difficult problem but should, nevertheless, prove a fertile field for investigation. For one approach to this problem see Hayne (1950).

It should be mentioned here that the season of collection might have affected the means of the samples. The method of age grouping employed would tend to offset differences of age composition of the populations from season to season, but even with voles of similar age, there could be phenotypic effects of seasonal environmental differences. In the samples at hand, however, there seemed to be no clear-cut relationship between the means and date of collection. In the graph (Fig. 5) some seasonal effects are no doubt confounded with geographic effects, but the latter are almost certainly significant in themselves. In any event, it was evident at this point that additional procedures would be required for a more satisfactory interpretation of the results; and the methods of covariance analysis, discussed in the following section, appear to furnish a satisfactory approach to this problem.

COVARIATION

Method and concepts. "Every growing organism, and every part of such a growing organism, has its own specific rate of growth, referred to this or that particular direction; and it is by the ratio between these rates in different directions that we must account for the external forms of all save certain very minute organisms." The foregoing statement by Thompson (1942: 82) implies that growth may be allometric and therefore that the ratio between two parts may change with age and size. This changing relationship between the dimensions of two parts was given a mathematical formulation by Huxley (1924; 1932). If x represents the size of a whole and y the size of a part, the relation between the two may be approximated by:

$$y = bx^a \dots\dots\dots (1)$$

The constant a represents the ratio between the geometric rates of growth of x and y and is termed the *relative growth rate*. Unless a is unity, growth will be allometric. The biological significance of b , which is termed the *initial growth index*, appears to be less clearly determined. Mathematically it represents the value of y when x is unity. Biologically it would seem to be a function of the ontogenetic point when growth (or a phase of growth at a given growth rate) begins in the element or dimension y ; but its validity

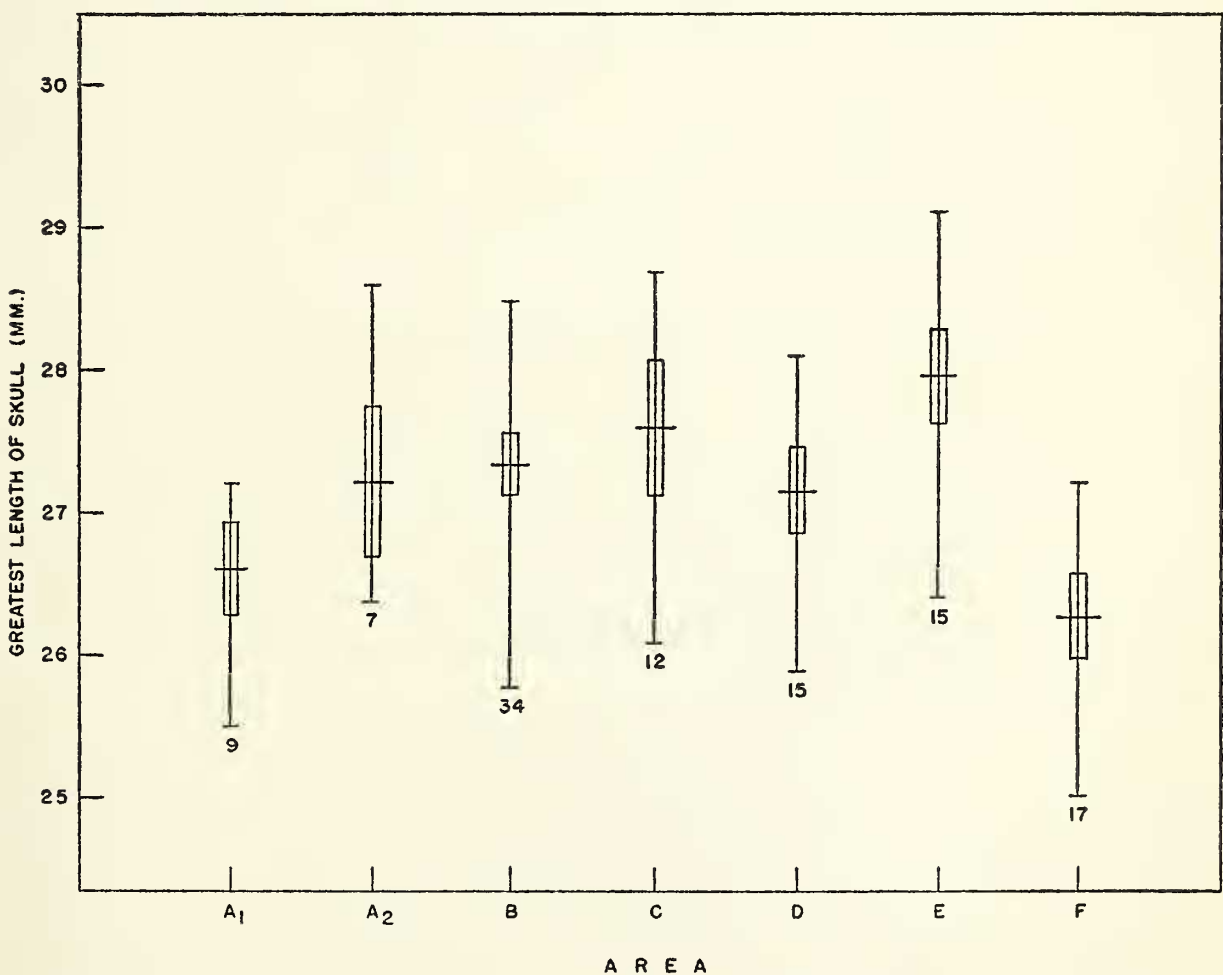


FIG. 5. Skull length of male *Microtus p. pennsylvanicus*, seven samples from northwestern Pennsylvania. Range and standard error shown as in Fig. 2.

or reality as such a constant depends on the proper choice of a unit in which to express x . Further discussion of the biological significance of these constants may be found in the work of Lumer (1936) and Lumer, Anderson, and Hersh (1942).

TABLE 2

Analysis of variance of certain dimensions in male *Microtus p. pennsylvanicus* from seven localities in northwestern Pennsylvania. F , variance ratio; n_1 , degrees of freedom for area mean square; n_2 , degrees of freedom for individual mean square.

	n_1	n_2	F
Total length	6	113	8.98**
Tail length	6	112	4.31**
Hind foot	6	202	23.57**
Ear	6	112	11.37**
Weight	6	97	8.29**
Greatest length of skull	6	102	11.40**
Condylzygomatic length	6	101	8.18**
Length of nasal	6	98	3.67**
Length of incisive foramen	6	112	5.06**
Length of diastema	6	112	12.47**
Length of rostrum	6	100	8.83**
Cranial breadth	6	174	1.50
Interorbital breadth	6	197	3.02**
Zygomatic breadth	6	103	7.20**
Cranial height	6	117	2.93*

* Probability between 5% and 1% levels

**Probability beyond 1% level

It is obvious from equation (1) that unless a has a value of one the ratio of x to y , as well as the absolute value of y , changes as x changes. This is one way in which a difference in proportions between two populations may be the result of absolute-size differences. On the other hand, the y values and consequently the ratios of x to y may differ from one population to another even though the x values are the same. This is truly a difference in proportion, not a function of size, and may result from either a difference in the relative growth rates, a , between the populations or a difference in the initial growth indexes, b , representing differences in the ontogenetic points at which growth begins.

By an analysis of covariance in which sample data from two or more populations are fitted to the curve defined by equation (1), we can determine whether or not differences exist among the populations in either the relative growth rates or the initial growth indexes. Reeve (1940; 1941) in a study of New World anteaters has demonstrated the methods for this procedure and worked out suitable probability tests. Tanaka (1952 and his earlier papers cited therein) has also used this approach in rodent systematics. Differences in relative growth rates are called by Reeve "differences in slope," and the test for their significance he termed the "slope test."

This test involves fitting the data to two sets of lines and then determining whether one set gives a significantly better fit. One set is made up of independent regression lines, one for each population. The other set is the best-fitting series of parallel lines, again one line for each population. If deviations from the latter set are not significantly greater than deviations from the former, no slope differences between the populations have been demonstrated.

The differences in initial growth indexes can not very well be tested directly since we do not know the size either at the starting point of growth or at any subsequent points when a change in rate may have occurred. Furthermore, the value of this constant, as already mentioned, depends on the unit in which it is measured and is therefore a variable figure. However, differences in values of y between samples which have the same x values and no slope differences, must be directly related to differences in the initial growth indexes. Such differences in y values can easily be calculated by the growth formula for the mean or any other specified value of x and are called by Reeve "differences in position." Accordingly the significance of these differences is determined by a "position test." The test again consists of a comparison, this time between the best-fitting set of parallel lines and the best-fitting single line. If the parallel lines give a significantly better fit, it is assumed that the means of the separate samples, which the parallel lines represent, show significant differences among themselves. Hence, since the mean of dimension x has been made the same in each sample, proportional differences may be assumed to occur among the populations. If a single line gives as good a fit as the parallel lines, there is no reason to assume such differences among the populations. In making the position test we make x the independent variable and thus eliminate all differences in this variable. Some information about variation in x is therefore unavoidably lost or covered up in order to make better use of that available with respect to y .

The position test can normally be used only when the slope test shows no significant differences in the relative growth rates. If there are growth rate differences, interpretation of positional differences becomes uncertain. The value of these tests is best indicated by quoting from Reeve (1940: 69). "It is evident from these examples that the proposed statistical tests do not make possible a full analysis of the nature of proportional differences between groups of animals, for whereas they provide an answer to the question 'Are there significantly large differences in relative growth-rate?' the question 'Are there differences in initial organ-size?' can as a rule only be answered when no differences in relative growth-rate appear. But this limitation need not worry the systematist unduly, since he will only want to know whether his data support the hypothesis that the proportional differences between the groups of animals under comparison are merely the result of absolute size-differences. The described tests appear to be admirable for this purpose." These statistical tests described by Reeve are similar to those given by Snedecor (1946: 318 ff.) for covariance analysis, but the

terminology is different. The position test of Reeve is the same as Snedecor's test for differences in adjusted means; and Reeve's slope test is equivalent to the test for significance of regression coefficients of Snedecor. Reeve's terminology will be used in the following discussion.

Davenport (1934), Richards (1935), Bernstein (1934), and others questioned the validity of the above formula for the study of growth relationships. They held that small changes in growth rate are obscured by the methods of treatment and that the value obtained is an average one, perhaps without much significance. Richards (1935) argued that the value of a , the growth rate constant, changes frequently during the life of the individual and he presented graphs to demonstrate this. However, he gave no indication of the standard deviation of his values; in the case of the graphs dealing with rats it would seem, on the basis of the original data which he apparently used (See Moment, 1933), that the samples were rather small. If so, the fluctuations which he found in the values of a are possibly not significant. Needham (1934: 83-84) observed that in some instances deviations found in values of a lost significance when a larger mass of data was employed in the calculation. It should also be mentioned that deviations in calculated values of a can result from variation between individuals as well as between different ages in the same individual. Granted, however, that a may vary somewhat during growth and also between individuals, it can still be a reliable index of the average growth relationships between various elements at least over the period of time (age range) represented by the samples used in this study.

In 1942 Kavanagh and Richards analyzed the status of the allometric equation and discussed the suitability of the different types of data which have been used in applying the formula to growth studies. They suggested that data of the type used in the present study portray only relative size, and not relative growth since there is no time factor involved; but if we assume that a certain portion of the variation within a group of individuals of similar age results from differences in stage of development, then there is a biological time factor. Thus it should be possible to consider the values of a and b as average growth constants for the population sampled. Kavanagh and Richards recognize this possibility but do not feel it can be accepted without more investigation. This is no doubt a valid objection in growth studies, since according to Merrell (1931), a growth curve based on averages of individual observations may not be characteristic of the actual growth curve of any particular individual. Therefore, study of a curve of averages would not likely lead to an explanation of growth processes. In taxonomic study, on the other hand, the situation appears to be reversed. Here we are concerned with populations and their parameters as much as, or even more than, we are with individuals. Thus, an average growth curve is perhaps a function of gene frequency, which is a population characteristic, and is therefore more important than an actual growth curve for any particular individual.

A note of caution should be added here. Recently Zuckerman and others (1950) published a critical discussion of methods used in growth studies.

It is apparent from this series of papers that a solid theoretical basis for the explanation of growth and form is still lacking. Much of the work at this time is of an empirical nature, and it is therefore generally unsound to extrapolate very far beyond the observational data.

There remains a somewhat technical difficulty in the use of equation (1). When growth is positively allometric and continues to follow the formula, $y = bx^a$, a point can eventually be reached when y is greater than x . When only linear dimensions, taken in different planes, are compared, no problem arises. But if one linear dimension, y , is a part of the other, x , or if the mass of one part, y , is compared to that of the whole, x , the theoretical implications are obviously more complex. This difficulty could be avoided by use of the equation, $y = b(x-y)^a$. However, as Needham (1934) pointed out, growth is not infinite and eventually either the value of a changes or growth stops at the adult condition. For practical purposes the values of a determined by the two equations appear to be quite similar (Needham, 1934) and the simpler form is used in the following calculations. It should be remembered, however, that this equation will not necessarily lead to meaningful correlation coefficients in those cases where the dependent variable, y , is a part of the independent variable, x , as, for example, in the comparison of length of diastema with total length of skull.

In application of the methods to the present study the simple allometry equation (1) discussed above is assumed to be a satisfactory approximation of the average growth relationships over the ages represented by the samples used. A linear function, $y = a + bx$, could be fitted to the data with an equally good correlation in some instances. However, the use of this equation would imply that growth is never allometric, the relative growth rate, a , having a value of one in all cases, and such an assumption is unrealistic in view of much experimental evidence (Huxley, 1932; Needham, 1934; deBeer, 1940; Carter, 1951). Thompson (1942: 205-212) evidently believed that growth followed the allometric formula as an exception rather than a rule, but Bonner (1952: 136) in his essay on morphogenesis disagreed, pointing out that the equation does fit numerous and diverse instances of growth. In the present study the relatively good correlation on the basis of a linear growth relationship results from the restricted range in size of the individual specimens in the samples. With the inclusion of a greater age range (and hence greater size range) in the data, the deviation from linearity would be expected to increase.

The actual calculations were based on the logarithmic form of the formula:

$$\log y = \log b + a \log x \dots\dots\dots (2)$$

The best-fitting curve for this form of the equation may be slightly different from one derived directly from equation (1), but the discrepancy should not be great. Furthermore, if growth is multiplicative, as we must assume to use the formula at all, the logarithmic form would actually appear to be the more fundamental and therefore the correct one to use (Reeve, 1940: 57). Perhaps the logarithmic rather than arithmetic values of the measurements

tend to be normally distributed (See, for example, discussion by Teissier, 1948: 27).

The procedure is illustrated graphically in Fig. 6 in which the logarithm of length of diastema is plotted against the logarithm of length of skull. Open circles indicate individual specimens; the solid circles represent the means of the various samples. Since, as will be discussed below, the slope was found to be similar for each sample, the individual regression lines are considered to be parallel and have been combined into one average line indicating the general trend. The slope and position of the line are calculated by the method of least squares as described by Reeve (1940) or by Snedecor (1946: 318 ff.). The procedures outlined by them are well suited to the analysis since they give not only the regression line but also lead directly to the significance tests mentioned above.

It will be remembered that in equation (1), b is the value of y when x is unity. The same relationship holds in equation (2) in which $\log b$ represents the point where the regression line crosses the $\log y$ axis at which time $\log x$ is equal to zero and x is unity. If calculations were carried out in millimeters, the constant b would thus represent the value of y for a skull length of one millimeter. This seems an unwarranted extrapolation of the growth curve to a very early (or probably non-existent) period of embryonic life. However, if dimensions are expressed in centimeters, b becomes the value of y when the skull is one centimeter in length. This skull size would correspond to a period some time after birth, and if a should be found to be constant from that time on, b would take on more biological significance. A still better unit of measurement might be arrived at if information were available concerning the points during growth where a might possibly change in value; but lacking this, centimeter units are believed to be satisfactory.

Experimental design. An analysis has been carried out on samples from 12 populations representing 12 different areas in Pennsylvania. The collecting localities within each area are given below.

<i>Area</i>	<i>Localities</i>
A.	Erie Co., East Springfield; 4½ mi. SW. of Northeast.
B.	Crawford Co., Linesville; 4 mi. SE. of Linesville; 2 mi. SW. of Linesville.
C.	Warren Co., 2½ mi. N. of Kinzua.
D.	Beaver Co., ½ mi. NW. of New Galilee; 1 mi. NE. of Darlington.
E.	Beaver Co., 2 mi. E. of Industry.
F.	Butler Co., 2 mi. E. of Mars; 3 mi. E. of Mars; 2 mi. W. of Saxonburg.
G.	Fayette Co., 2 mi. NW. of Markleysburg. Somerset Co., 4 mi. SW. of Somerset; 5 mi. WNW. of Salisbury. Westmoreland Co., 4 mi. SE. of Laughlinton; 3 mi. SSE. of Rector; ½ mi. NE. of Rector.
H.	Lycoming Co., 3 mi. SW. of Montgomery; 1½ mi. S. of Nisbet; 2 mi. SE. of Trout Run. Montour Co., 2 mi. WNW. of Danville.

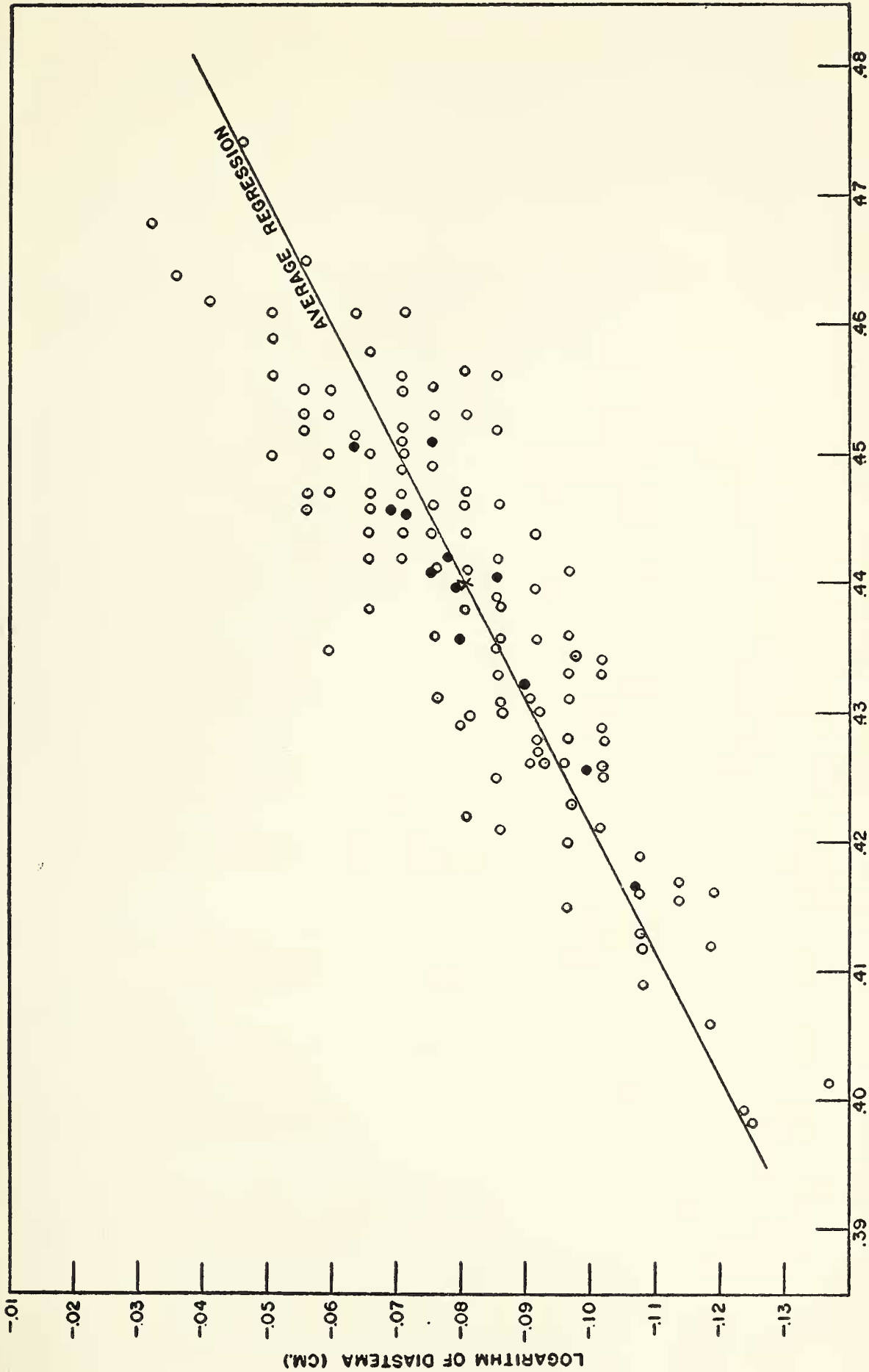


FIG. 6. Regression of logarithm of diastema on logarithm of skull length of male *Microtus p. pennsylvanicus*. Open circles indicate individual specimens; solid circles show sample means; general mean shown by X on the regression line which is an average of the separate lines which could be drawn for the 12 samples plotted.

- Northumberland Co., 1 mi. S. of Montandon; 2½ mi. SW. of Riverside.
- I. Bedford Co., 5 mi. NE. of Chaneyville; 5 mi. ESE. of Chaneyville; 1½ mi. NE. of New Paris.
Fulton Co., Crystal Spring; Fort Littleton; 3 mi. W. of McConnellsburg; 2 mi. E. of Warfordsburg.
Huntingdon Co., 1½ mi. SE. of Orbisonia; 1 mi. NE. of Spruce Creek.
- J. Adams Co., 1 mi. S. of East Berlin.
Cumberland Co., 1 mi. W. of Plainfield.
Franklin Co., 1½ mi. SE. of Fayetteville; 6 mi. NNW. of Chambersburg; 4 mi. E. of Greencastle; 2 mi. NE. of Mont Alto.
York Co., 5 mi. NNE. of Hanover.
- K. Monroe Co., Pocono Lake; 2 mi. NW. of Pocono Lake; 2 mi. NNW. of Pocono Pines; 1½ mi. SSE. of Tannersville.
Pike Co., Bruce Lake; 2 mi. NE. of Bushkill; 5 mi. SE. of Greentown.
- L. York Co., 2½ mi. NE. of Delta; 3 mi. N. of Delta.

These 12 areas represent quite diverse environmental situations both physiographically and biologically. It was mentioned earlier that it would eventually be necessary to know how much this environment affects the characters on which our taxonomic conclusions are based. It would be desirable to know also how much of such environmental influence is exerted directly on each individual and how much has been incorporated by selection into the genetic matrix of each population. These questions, however, are beyond the scope of the present paper. Here it has been necessary to confine the study to determination of the amount and nature of the variation among populations with respect to their spatial arrangement only. Except for the suggestion, pointed out below, that differences in growth constants are likely to reflect genetic differences, the study does not attempt to determine the causes of the variation. A conclusive investigation to determine the relative effects of the various factors which produce the variation remains to be carried out.

Each of the above samples (A-L) contained 11 specimens (males only) primarily of age groups 9 through 12, although in a few cases individuals of age group 8 were included. This was necessary since it was desirable for computational purposes to have specimens complete in all dimensions, and not enough of the older ones were available. This fact also explains why more samples were not included in the analysis and why some samples represent such large areas. There were not enough of the older and intact skulls available to make up more and larger samples. More than seven hundred skulls were examined in order to select the 132 making up these 12 samples. Most of those not used were young specimens; a few were damaged. There were some additional intact adult skulls, but they came from areas where the number of specimens was too few to make up a sample and the locality was too isolated to include within another sample. The age range was restricted as much as possible in order to reduce the chance

of including young specimens the growth of which might be at a different a value. If it were not for this possibility, a greater age spread could be utilized since under a given value of a , similar changes in proportion are considered to have taken place in individuals which have reached the same size even though their ages may be different.

In the case of two skulls which were used in the analysis, one dimension could not be measured because of a broken part. The missing values were calculated from the remaining data and the degrees of freedom reduced accordingly. In these instances the resulting calculated values were quite similar whether obtained by regular regression methods or by the minimum error method of Fisher (1949). The latter is perhaps better for the purpose since it minimizes the errors of estimate of y .

Length of skull was chosen as the independent variable, x .* In an analysis of covariance, seven other dimensions were used successively as the dependent variable, y . One of these, interorbital breadth, showed no significant correlation with skull length within the size range of the samples; and since a separate analysis of variance indicated no significant variation of the absolute size of this dimension throughout the state, further analysis of this measurement was eliminated. Of the other six dimensions three were measurements of length (diastema, rostrum, and incisive foramen), two were measurements of width (cranial breadth and zygomatic breadth), the remaining dimension was cranial height.

The 12 samples were next placed in four groups, with three samples in each group. The areas represented by the samples and the arrangement in groups is shown by the map, Fig. 7. In the analysis, each group was first considered as a sample of 33 individuals and tests were made for differences among groups. Following this, the areas were used as the sample units and differences among areas within each group were tested.

From the foregoing discussion it will be seen that with the design outlined, we can obtain information on two aspects of geographic variation: (1) variability present within small geographic areas in comparison with the amount of variability in relatively much larger areas; (2) amount of variability resulting from differences among populations in growth constants, either the relative growth rate, or the initial growth index. Such variation in growth constants is believed by some workers (Huxley, 1932; Reeve, 1940) to be

*In studies of relative growth with the type of data here available such an independent variable is not justified according to Kavanagh and Richards (1942). This criticism could be overcome by using methods described by Teissier (1948) or by Kermack and Haldane (1950) in which both variables are subject to error. Reeve (1950) has recalculated the growth rate coefficients in anteaters according to Haldane's method; he obtained somewhat higher values than originally, but the differences were not such as to change his interpretations. The disparity in results obtained by the different methods obviously depends on the correlation between the dimensions—the higher the correlation the more nearly alike will be the calculated growth rate coefficients. In the present study the usual method seems to be a valid one since the primary purpose is to predict, for each sample, probable values of the variables for a particular length of skull. However, it should be kept in mind that the constants a and b will not have the same values as if calculated without an independent variable.

evidence for the operation of genetic factors, and for some cases this has been definitely demonstrated (See discussion by deBeer, 1940: 365-393). It is presumed that environmental effects show up mainly in differences in absolute size, to which genetic factors no doubt contribute also. The apparent geographic irregularity in length of skull in such a widely distributed (and supposedly broadly interbreeding) species as *M. pennsylvanicus* might lead one to suspect that environmental factors account for much of the variability in absolute size; but, if hereditary factors are involved, it might be equally argued that genetic mechanisms could cause the same irregularities.

Significance tests. Tests were first made for slope differences by the method described above. Neither the four group regressions nor the 12 area regressions showed any significant variation in slope. Thus, further tests are concerned only with positional differences, and regression lines for individual samples may be considered parallel.

In making the position tests for differences in proportion the method of Reeve, described briefly above, has been extended to take advantage of the hierarchical classification of the samples into groups and then into areas within the groups. Because of this arrangement the data can be combined in several ways in making the tests. Two of these appear to be pertinent here.

Test 1. Deviations from a single line fitted to the 132 individuals are compared with deviations from four parallel lines each representing regression within a group and each based on 33 individuals. If the four lines give a significantly better fit than the single line, differences among the four populations is indicated; and we can assume that geographic variation, involving proportional differences occurs within the state. If the four lines give no better fit than the one, geographic variation in proportions among the four groups has not been established. This test is illustrated by the calculations for diastema in Table 3 and follows the procedure of Snedecor (1946: 320).

Test 2. The pooled deviations from the four parallel lines are compared with the pooled deviations from 12 parallel lines each representing regression within one area and each based on 11 specimens. If the 12 area lines give a better fit than the four group lines, there is variation among the areas within the groups. Further analysis of each group separately (by the method of Test 1) will then determine whether this variation occurs within all groups or only certain ones. The steps involved in Test 2 are again illustrated by the diastema in Table 4. There may be some question as to the validity of this procedure.* I have seen no mathematical treatment in which the data are combined in this fashion in making a covariance analysis; however, the test appears to be a logical one.

*For this particular case, the question is, however, an academic one. The results of Test 1 show that the four lines give no better fit than one line. Thus instead of Test 2 the comparison could actually be made between the 12 parallel lines and one line, and the procedure then becomes similar to Test 1. Such a comparison was made for each dimension and in every case the results were similar to those obtained by Test 2.

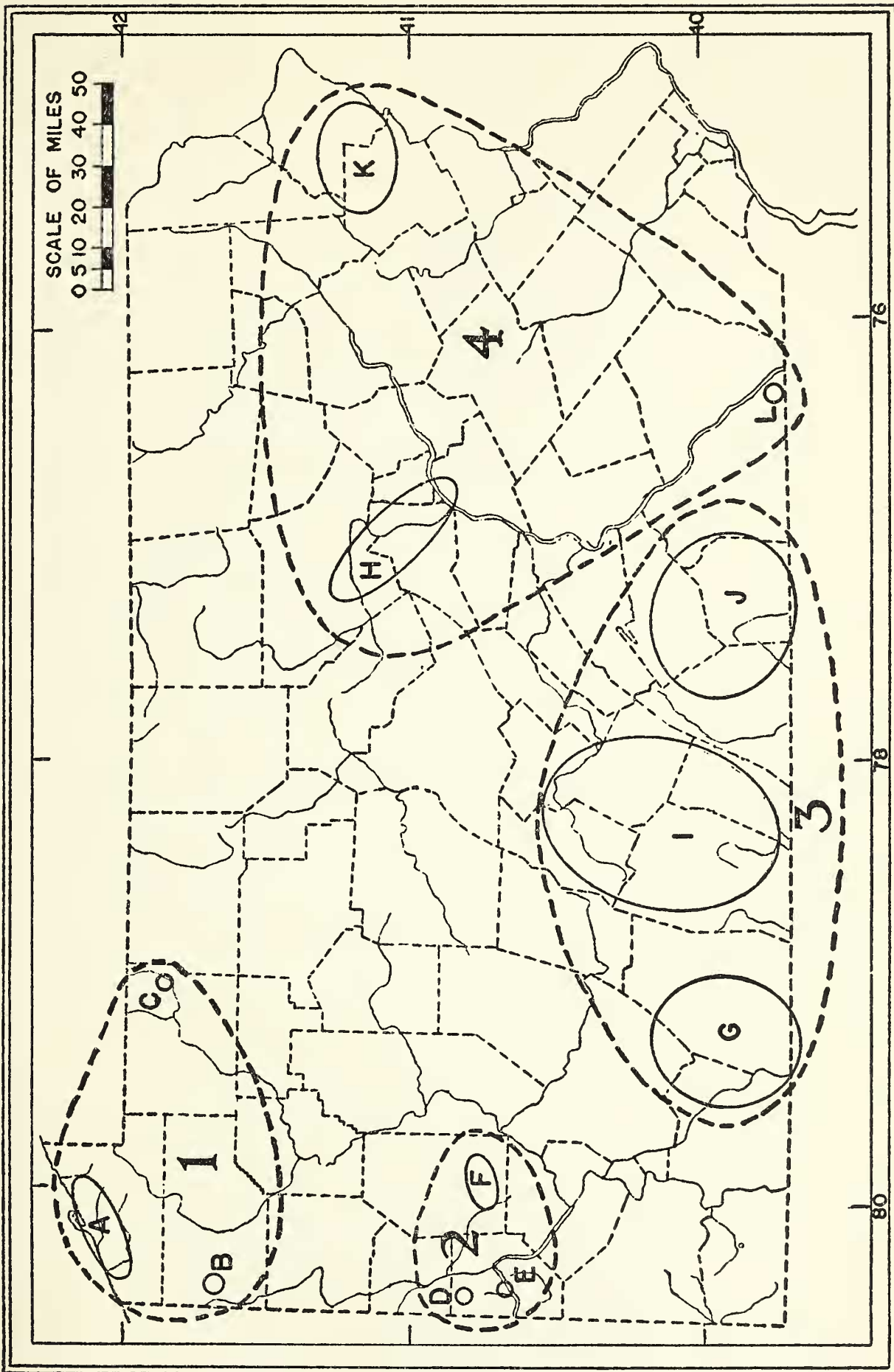


FIG. 7. Areas represented by the samples used in covariance analysis of skull variation in *Microtus p. pennsylvanicus* in Pennsylvania. Groups indicated by 1-4. Areas indicated by A-L.

In addition to the above tests which make use of covariance analysis, we can also make an analysis of variance in which each dimension is tested independently, no regression being involved. The tests are somewhat similar to 1 and 2 above, the difference being that deviations are calculated from the respective means rather than from the regression lines. This latter analysis does not serve as a test for proportional differences; the purpose here is to determine whether differences in absolute size exist. These tests follow the usual variance analysis procedure and need not be illustrated.

Results. The analysis of variance indicates that skull length varies among groups. The means of group 3 and group 4 are the larger, and this may be an indication of a cline in which absolute size increases toward the south and east. There is also variation among areas within groups. A test of each group separately further shows that only in group 2 (areas D, E, and F) are these differences among areas significant. Thus most of the variation in skull length among areas can be traced to this group. Of the other dimensions, cranial breadth, rostral length, and length of diastema exhibit variation among groups; the remaining three do not. However, all except cranial breadth show variation among areas within groups. As in the case of skull length much of this among-area variation can be traced to group 2, but group 1 appears to contribute a considerable amount also. These results from variance analysis for differences in size are shown in Table 5. Columns 3 through 6 give the significance of differences among areas within each group separately; column 7 indicates variation among areas in the combined groups; column 8 gives variation among groups with the areas left out of consideration.

At this point the data indicate that the populations differ in absolute size with possibly a clinal trend. Before drawing any further conclusions it is necessary to carry out the position tests for proportional differences by means of covariance analysis. The results of these tests are perhaps surprising. The size variation among groups can be explained by regression on skull length. In no case do the four group lines give a significantly better fit than one line. Thus, although there are differences in the absolute measurements among the groups, no proportional differences have been demonstrated; but among areas within groups some of the variation in absolute size is independent of variation in skull length. This is true for all dimensions except cranial breadth. Thus proportional differences exist among areas within the groups. It is of interest to note, however, that among samples of group 2, which show the greatest amount of variation among areas in absolute size, but which are separated by a maximum distance of about thirty miles, proportional differences are much less. Almost all the variation in this group is explained by regression on length of skull. Only the incisive foramen, one of the most variable dimensions (See Table 1), shows proportional differences. These results from the analysis for variation in proportion (position differences) are shown in Table 5. As in the case of size differences, columns 3 through 6 are for the separate groups, column 7 gives the results for the combined groups, and column 8 shows

TABLE 3

Comparison of errors of estimate from the best-fitting set of four parallel lines with errors from the best-fitting single line. Regression of diastema length on greatest length of skull in male *Microtus p. pennsylvanicus* from Pennsylvania.

Source of variation	Degrees of freedom	Sums of squares and products			Errors of estimate		
		Σx^2	Σxy	Σy^2	Sum of squares	Degrees of freedom	Mean square
Total	131	0.030107	0.032780	0.047398	0.011708	130	
Among groups	3	0.005292	0.006248	0.007599			
Within groups	128	0.024815	0.026532	0.039799	0.011431	127	0.000090
			Difference		0.000277	3	0.000092

$$F = \frac{0.000092}{0.000090} = 1.02$$

the variation among groups. The calculation for column 7 was illustrated in Table 4; that for column 8 in Table 3.

This situation in which differences in proportion occur locally but not over a wider area poses a logical problem, but its explanation may be simple. It may mean merely that variation in proportion is local and not clinal; the large samples (groups) being heterogeneous would tend to smooth out the differences between the smaller samples (areas). Under this assumption each local population would have, for a given characteristic, its particular range and frequency of phenotypes reflecting in part at least the gene frequencies. If there were a geographic cline, the frequency peaks would not only exhibit local variation but would shift in a regular fashion with distance. This would be evident in a shift of the means from one sample to another along the direction of the cline, especially if each sample included several adjacent local populations. This is what seems to occur in absolute size of skull within Pennsylvania. If there were no cline, the frequency peaks would continue to vary locally but would show no geographic trend. In this case, the means of large samples including several local populations would tend to be the same. The skull proportions appear to vary in this manner. This study does not fit such a model perfectly because some of the samples cover so much geographic area as perhaps to be heterogeneous themselves.

These conclusions do not indicate that large samples covering relatively large areas are not valuable for describing average characteristics of a given species or subspecies. However, they do point to the probability that the local populations are the more basic units. This corroborates what has been evident for some time—that populations differing considerably in absolute size and in proportions may occur within such a small area that formal recognition of them as geographic races or subspecies is neither practical nor desirable. Nevertheless, in studies of wider geographic scope, knowledge of these local variations is very desirable, since clinal trends may be obscured if some of the collecting localities happen to represent extreme local populations. Furthermore, the magnitude of variation between these local populations may approach that occurring between recognized subspecies thus destroying the objective basis of delimitation of these geographic races.

Summarizing these results we may say that variation in size among the populations is produced (1) by variation in factors operating on the skull as a whole thus affecting absolute size, perhaps in a clinal fashion; and (2) by variation in allometric factors which affect proportions within the skull. In the second case no clinal trend is evident within Pennsylvania. In those dimensions where variation in size can be explained by regression on skull length, allometric factors evidently remain constant (for the dimensions involved), and variation in absolute factors alone need be postulated. These factors of size may have a genetic basis, but they could equally well be caused by age, seasonal, or environmental effects. On the other hand, where both absolute and proportional differences occur, allometric factors as well as absolute size factors must differ among the populations. These allometric factors could also be environmental but in the present state of our knowledge they seem to provide a safer indication of hereditary variation

TABLE 4

Comparison of errors of estimate from the best-fitting set of 12 parallel lines with the errors from the best-fitting set of four parallel lines. Regression of diastema length on greatest length of skull in male *Microtus p. pennsylvanicus* from Pennsylvania.

Source of variation	Degrees of freedom	Sums of squares and products			Errors of estimate		
		Σx^2	Σxy	Σy^2	Sum of squares	Degrees of freedom	Mean square
Total	131	0.030107	0.032780	0.047398			
Among areas	11	0.012511	0.014445	0.018851			
Within areas	120	0.017596	0.018335	0.028547	0.009442	119	0.000079
Within groups (from Table 3)	128	0.024815	0.026532	0.039799	0.011431	127	
Difference					0.001989	8	0.000249

$$F = \frac{0.000249}{0.000079} = 3.15^{**}$$

than does the presence of absolute size differences alone. Another advantage of the method used here is that we can take into account such things as slight age differences which we know are present and probably affecting size but which we can not otherwise readily compensate for.

As an aid to interpretation, the means of the skull lengths as well as the means of the other dimensions (adjusted for the differences in skull lengths) are graphed in Fig. 8 for each population sampled. This gives a picture of (1) overall variation in size (as far as this is shown by skull lengths) and (2) variation in other dimensions with the effect of skull length differences removed.

The geographic arrangement is indicated on the graph. In addition, within each of the three sections of Pennsylvania (western, central, and eastern) the samples from left to right represent north to south populations. Thus major trends in either east-west or north-south directions could be detected if present. Study of this figure leads to the same conclusion as we drew from the summary in Table 5, that there are special factors causing proportional variation within the skull; but it is now made more evident that this variation is not particularly clinal or a function of distance, since no obvious trends are recognized.

TABLE 5

Results of significance tests of variation in absolute size (standard type) and in proportion (*italics*) in the skull of male *Microtus p. pennsylvanicus* in Pennsylvania. *S* indicates significance, and *0* indicates no significance at the 0.05 level of probability.

Dimension	Kind of variation	Among areas within groups					Among groups
		1	2	3	4	All	
1	2	3	4	5	6	7	8
Greatest length of skull	size	0	S	0	0	S	S
Zygomatic breadth	{ size proportion	S S	S <i>0</i>	0 <i>0</i>	0 <i>0</i>	S S	0 <i>0</i>
Cranial breadth	{ size proportion	0 <i>0</i>	0 <i>0</i>	0 <i>0</i>	0 <i>0</i>	0 <i>0</i>	S <i>0</i>
Cranial height	{ size proportion	0 <i>0</i>	S <i>0</i>	0 <i>0</i>	S <i>0</i>	S <i>0</i>	0 <i>0</i>
Length of diastema	{ size proportion	S S	S <i>0</i>	0 S	0 <i>0</i>	S S	S <i>0</i>
Length of rostrum	{ size proportion	S <i>0</i>	S <i>0</i>	0 S	0 <i>0</i>	S S	S <i>0</i>
Length of incisive foramen	{ size proportion	S S	S S	0 <i>0</i>	0 <i>0</i>	S S	0 <i>0</i>

In order to indicate the importance of variation among local populations, samples from other populations of *Microtus pennsylvanicus* in northeastern North America were measured and the means plotted in Fig. 8. As above, skull length is plotted to show variation in absolute size; the other dimensions to show variation in proportion. The samples were allocated to the following subspecies on the basis of Hall and Cockrum (1953): *pennsylvanicus* from Ontario (Peterboro, Kent, and York counties), *fontigenus* from Ontario (mouth of Moose River), and from southeastern Quebec (St. Margaret, Natashquan, and Kegashka rivers), *enixus* from Labrador (Red Bay, Battle Harbor, Windsor, Nain, and the Hamilton River), *labradorius* from Quebec (Nastapoka, Koaksoak, and Great Whale rivers). It is somewhat surprising to find that these populations are quite similar to those in Pennsylvania. Although only relatively small series have been measured, these were (as in the case of the Pennsylvania specimens) selected from a much larger number the great majority of which were immature. The samples should therefore be more representative for our purpose than a larger series containing many younger age groups. It is evident from the graph that with few exceptions the means of the samples of *fontigenus*, *enixus*, and *labradorius* as well as the Ontario *pennsylvanicus* are within the range of the means of the samples from Pennsylvania. The greatest deviation from the Pennsylvania material is shown by the length of diastema in the sample of *enixus*; and in this case the difference is just on the borderline of the commonly accepted level of significance.

It appears that, on the basis of the skull characters used here, samples such as these could not be properly placed with regard to subspecies without a knowledge of the geographic location of the specimens. Since these samples do not constitute topotypical material, no inferences are drawn regarding the validity of the subspecies. Furthermore, other characters could no doubt be found by which these populations could be recognized under prevailing concepts. It may be noted though that Weaver (1940) who had topotypical material of both *pennsylvanicus* and *fontigenus* did not regard the latter as a valid subspecies and referred his specimens from the southern coast of the Labrador peninsula to *pennsylvanicus*. However, the problem presented by these results is not one of finding characters to separate various forms but of arriving at a clear-cut and unambiguous basis for erecting a subspecies. It will probably always be possible to find differences between any two populations; the difficulty is in deciding when the differences are important in relation to the end in view. Perhaps it is time to re-examine the basic concepts by which we continue to describe and recognize mammalian subspecies in order to determine just what is "the end in view." Then we can arrive at some conclusions regarding the purposes and values of infraspecific categories—purposes and values which should benefit the phylogenist as well as the nomenclaturist.

Perhaps the growth constants themselves are of more general interest to biologists than the foregoing remarks which may have little appeal to other than systematists. These constants are given in Table 6. All figures are carried to five decimal places, the maximum number which are significant.

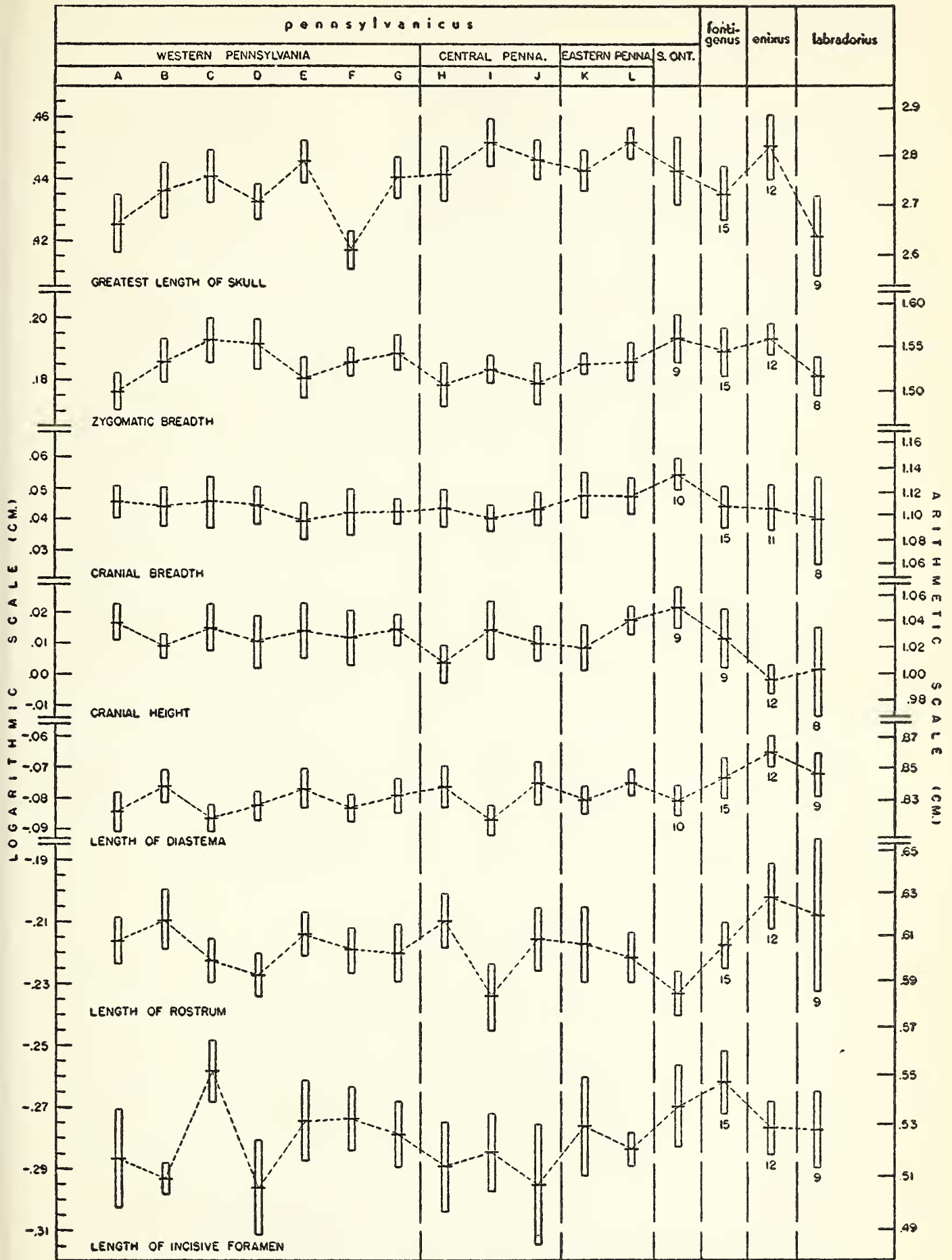
FIG. 8. Variation in skull dimensions of male *Microtus pennsylvanicus* from northeastern North America. The rectangle indicates two standard errors on either side of mean which is represented by the heavy horizontal line. For greatest length of skull the mean is given as computed from the absolute measurements; and the standard errors are estimated by the formula

$$s_{\bar{x}} = \sqrt{\frac{\sum x^2}{n(n-1)}}$$

where x is the deviation of an individual from the mean and n is the number of individuals in the sample. For all other dimensions the means have been adjusted to correspond to a common skull length, in this case the overall mean of the Pennsylvania specimens, 0.43894. The standard errors are estimated by

$$s_{\bar{y}} = \sqrt{\frac{\sum d_{y.x}^2}{n(n-2)}}$$

where $d_{y.x}$ is the deviation of an individual from regression. Each sample contains 11 specimens except where otherwise indicated by number under rectangle.



The values of a are given along with their standard errors. It will be seen that for incisive foramen and diastema the constants are not significantly different from unity. Thus, the regressions of those dimensions on skull length are essentially rectilinear, whereas the other dimensions exhibit a curvilinear regression on skull length since the values of a are, with the possible exception of zygomatic breadth, almost certainly other than unity. It might be noted that allometry is negative for the dimensions of width and height and definitely positive only in the case of rostral length.

As we have already seen, the initial growth indexes are much less stable than the relative growth rates and are of more difficult interpretation, but they are given as $\log b$ in the regression equations in Table 6 for the benefit of any who might wish to compare their results with those reported in this paper. Except for cranial breadth, in which there is no significant difference between means of the samples, $\log b$ in each formula represents an average of the values for the 12 populations. Thus the regression line is an average one and the line for any given population is above or below the average and parallel to it.

TABLE 6

Relative growth rates with their standard errors, and formulas for regression of various dimensions on skull length in male *Microtus p. pennsylvanicus* from Pennsylvania. Value of $\log b$ computed with the units of measurement in centimeters.

	Relative growth rate $a \pm s_a$	Regression equation $\log y = \log b + a \log x$
Zygomatic breadth	0.80081 ± 0.07871	$\log y = -0.16771 + 0.80081 \log x$
Cranial breadth	0.36364 ± 0.05703	$\log y = -0.11616 + 0.36364 \log x$
Cranial height	0.61228 ± 0.06586	$\log y = -0.25744 + 0.61228 \log x$
Length of diastema	1.04200 ± 0.06700	$\log y = -0.53887 + 1.04200 \log x$
Length of rostrum	1.41856 ± 0.11182	$\log y = -0.84310 + 1.41856 \log x$
Length of incisive foramen	0.94521 ± 0.16653	$\log y = -0.69847 + 0.94521 \log x$

SUMMARY AND CONCLUSIONS

A series of meadow voles, *Microtus p. pennsylvanicus*, from Pennsylvania was studied to determine the nature and amount of geographic variation with particular reference to the size and proportions of the skull.

The individual specimens were classified in age groups on the basis of relative development of the paroccipital process and of crests in the occipital region of the skull. It was found that the dimensions cranial breadth, cranial height, interorbital breadth, ear, and length of hind foot approach their maximum development at an earlier age than do the other elements considered.

Of the skull dimensions studied, greatest length, condylozygomatic length, cranial breadth, cranial height, and zygomatic breadth show the least individual variation within one population.

An analysis of 150 specimens from several localities in northwestern Pennsylvania indicated that in greatest length of skull males average approximately 0.4 mm. longer than females.

Analysis of variance among samples from seven populations in northwestern Pennsylvania showed that the total variation in all external and skull measurements, except cranial breadth, is significantly greater than might be accounted for by individual variation within each population. Thus, geographic variation in size within this relatively small area is evident.

Analysis, by covariance methods, of the size relationships between skull length and other dimensions showed that within Pennsylvania most of the variation in the skull of *Microtus p. pennsylvanicus* involves factors for proportional differences as well as factors for differences in absolute size. The variation in size shows a slight tendency to be of a clinal nature, but for the most part is quite irregular. The maximum range in size may be shown by populations within one or two counties. Factors of age, season, and environment could be important agents in this variation. Variation in proportion occurs among local populations but exhibits no demonstrable clinal trend within Pennsylvania.

Relative growth rates between the various dimensions and the skull length were found to be similar throughout Pennsylvania.

A comparison of the Pennsylvania material with series from other parts of northeastern North America showed that, for the characters studied, means of samples of *M. p. labradorius*, *M. p. enixus*, and *M. p. fontigenus*, were with few exceptions, not significantly different from, and in most cases actually fell well within, the possible range of mean values of populations of *M. p. pennsylvanicus* from Pennsylvania.

On the basis of the geographic variation observed in this study it is suggested that in systematic studies of wider geographic scope, knowledge of the extent and direction of local variation, both in size and in proportion may be of considerable importance for the correct analysis of clinal trends and recognition of geographic races.

It is further suggested that it would be desirable to re-examine our basic concepts of mammalian subspecies in order to arrive at an unambiguous usage and to clarify the purposes for which they are erected.

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